

Individual Differences in Color Vision

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As several of the chapters in this book illustrate, the characteristics of color vision vary widely from one individual to the next. These variations arise from a number of factors, including color deficiencies and disease (chapter 33), changes during development or aging (6, 9, 32), and the effects of language or culture (7, 8, 30). In this chapter, we focus on inter-observer differences that presumably reflect the inherent variability in the mechanisms encoding color or how they are influenced by experience, within “normal” adult observers who share a relatively similar culture and language. Even within such homogeneous groups there is a surprising diversity of color vision, manifest in many ways. Thus two observers can have very different sensitivities to wavelength; the physical spectra that match to one may be readily distinguishable to another; and the ways in which the same physical stimuli are labeled can differ markedly. To explore these differences, we will first review the range and causes of variations in spectral sensitivity, and the implications of these variations for defining color metrics and characterizing color mechanisms. We will then review the striking differences in color perception (or at least in how people label these percepts). Unlike spectral sensitivity, the bases for variations in color appearance remain enigmatic, but studies of individual differences have played a key role in understanding the nature of color experience and how it is shaped by characteristics of both the observer and their environment.

Individual differences and the mechanisms of color vision

Individual differences in perception are currently experiencing a revival of interest. One reason for this is the recognition that these differences provide information not only about the range of natural variability – nature’s experiments - but also an important tool for exploring the underlying mechanisms of perception (Wilmer, 2008). Part of this power comes from relating variations in behavior to variations in the observers themselves. A classic example is twin studies, which continue to provide powerful insights into the contributions of genetic and environmental factors to vision (Wilmer et al., 2010) and have been used to tease apart these factors in color vision (D. Bimler & Kirkland, 2004; Paramei, Bimler, & Mislavskaja, 2004). A further potent advantage is to compare how observers vary across tasks or conditions. Specifically, analyses of the distinct ways that two individuals might differ on a perceptual measurement can reveal the number and form of the distinct processes mediating their behavior. If performance on two tasks is related, they are likely to depend on a common limiting step, while independent variations would implicate that they are controlled by different processes. A recent example of this approach is the use of individual differences to show that sensitivity to S cone increments and decrements are only partially correlated, implicating both shared and distinct mechanisms contributing to the thresholds (Jenny M. Bosten et al., 2014).

Analyses of this kind applied to larger data sets are the basis of latent variable modeling approaches such as factor analysis. These use the pattern of correlations across a set of observed measurements to determine the underlying causal factors contributing to the variability. As an example, Webster and MacLeod (Webster & MacLeod, 1988) used factor analysis to examine

individual differences among the 49 observers tested in the 10 deg color matching study of Stiles and Burch. The 96 observed variables were the intensities of the 3 primary lights required to match 32 test wavelengths ranging from 392 to 714 nm. Matches at some wavelengths are highly correlated – e.g. an observer who requires more (than average) green primary at 500 nm will also require more at nearby test wavelengths, and these correlations reflect the common influence of potential physiological characteristics contributing to the measured inter-observer differences (e.g. differences in the density of screening pigments). Moreover, these measurements can be precise enough not only to identify the putative mechanisms but to define their specific characteristics such as their spectral sensitivity (MacLeod & Webster, 1988). Factor analytic approaches have also been used to explore the number and tuning of neural mechanisms underlying spatial and temporal and chromatic sensitivity and how these change during development (Dobkins, Gunther, & Peterzell, 2000; Gunther & Dobkins, 2002, 2003; Peterzell & Teller, 2000).

A related technique that has been widely applied to measures of color appearance is known as multidimensional scaling, in which similarity ratings among a set of stimuli are used to deduce the underlying dimensions on which observers judge the stimuli (again with the aim of reducing the observed settings to a smaller set of explanatory dimensions). In fact an early validation of the principles of multidimensional scaling were based on reconstructing the color circle from measurements of color similarities (Shepard, 1962). As described below, many studies have since applied this technique to explore the perceptual color spaces of different individuals or groups.

Sources of sensitivity variation

A number of factors combine to determine the spectral sensitivity of the visual system, and because each varies they collectively lead to large differences across observers. Many of these factors reflect processes at or before the level of the photoreceptors and are well characterized.

Prereceptor screening. The crystalline lens of the eye contains an inert pigment that selectively absorbs shorter wavelength light, and is a main source of sensitivity loss at short wavelengths, protecting the retina from UV exposure (van Norren & Vos, 1974). The density of the lens pigment varies widely across individuals, in part because the pigment itself increases with light exposure, and increases steadily with age (Pokorny, Smith, & Lutze, 1987). The brunescence of the aging lens is in fact a major cause of spectral sensitivity losses with aging (J. S. Werner, Peterzell, & Scheetz, 1990). Photoreceptors in the central retina are further screened by a second inert filter known as macular pigment, which resides in fiber layers of the retina and again primarily absorbs at shorter wavelengths. Average density at the wavelength of maximum absorption (458 nm) is ~0.5, but individual densities can differ by a log unit or more, and can vary widely depending on factors like diet (Davies & Morland, 2004). Moreover, the density peaks in the central fovea but falls rapidly with eccentricity, reaching negligible levels by a few degrees (Snodderly, Auran, & Delori, 1984; Wooten & Hammond, 2005). Thus the pigment is a major contributor to spatial variations in spectral sensitivity *within* the observer. The spatial distribution of the pigment can also vary across observers (Hammond, Wooten, & Snodderly, 1997). Factor analysis of color matching data suggest that differences in macular and lens pigment density are among the most important sources of individual variation in color matches, even when the fields are large (Webster & MacLeod, 1988). Figure 1 illustrates the magnitude of

differences in the chromaticities in retinal images that can occur from normal variations in the prereceptoral screening pigments.

Figure 1

Photopigments. Among normal observers spectral sensitivities of the cones can vary both in their spectral peak and spectral bandwidth. The peak absorption of the photopigments is controlled by a small number of loci in the genes coding the opsins (Neitz & Neitz, 2011). One intriguing variation in the L cone pigment is a common polymorphism at site 180. In the Caucasian population roughly 62% of the genes code for Serine while 38% code Alanine. The presence of Serine results in a 4-7 nm shift toward longer wavelengths in the the λ_{\max} of the opsin, a difference sufficient to produce a small but measurable shift in color matching (Winderickx et al., 1992). This difference is notable because it reflects the first case where a perceptual difference can be traced to the smallest functional change in the genetic code (J. D. Mollon, 1992), though in situ the discrete genetic change does not reflect a simple discrete dichotomy of in the λ_{\max} of observers (Webster, 1992). A still more intriguing potential variation is that the L and M genes are encoded on the X chromosomes, and thus some females inherit different versions of the L or M pigment genes on their two chromosomes (Neitz & Neitz, 2011). Early in development one or the other chromosome is inactivated, so that these females may express either variant of the genes in different classes of cones. This predicts that a large proportion of females in the normal population might actually be tetrachromats, sensitive to a fourth dimension of color (Jordan & Mollon, 1993). Higher-dimensional color vision in females has been shown to occur in many species of new world monkeys, where there is only a single longer-wave pigment coded on the X chromosome but with multiple alleles. In this case males are obligate dichromats, while a subset of heterozygous females can be shown behaviorally to be trichromats (J. D. Mollon, Bowmaker, & Jacobs, 1984). Some evidence has pointed to tetrachromacy in female carriers of anomalous trichromacy (Jameson, Highnote, & Wasserman, 2001; Jordan, Deeb, Bosten, & Mollon, 2010; Jordan & Mollon, 1993; Nagy, MacLeod, Heyneman, & Eisner, 1981). But thus far the existence of human females who are behaviorally tetrachromats has been difficult to establish.

Differences in bandwidth of the absorption spectrum – rather than in the peak - also occur and can arise from variations in the optical density of the photopigment. As density increases (for example with longer outer segments, higher pigment concentrations, or better absorption efficiency) the probability of photon absorption also increases because the receptor has more chances to catch a photon. This “self screening” has the largest effect near the tails of the spectrum where quantal catch is lower, thus broadening the absorption curve (Wyszecki & Stiles, 1980). These density differences contribute to individual differences in color matching, and photoreceptor inefficiencies are an important factor limiting visual sensitivity in early development (Banks & Bennett, 1988). Density differences are also enough to provide functionally distinct classes of receptors in some color deficient observers even when the classes have the same spectral peak (Neitz, Neitz, He, & Shevell, 1999).

Cone ratios. The color-normal population also exhibits striking differences in the relative numbers of different cone classes. On average, there are roughly twice as many L cones as M cones, with S cones making up only ~5 %. However, these ratios turn out to vary wildly from one observer to the next. L:M ratios have been reported to range from roughly 1:1 to 16.5:1

among observers who are normal trichromats (Hofer, Carroll, Neitz, Neitz, & Williams, 2005). The cone mosaic can now be directly imaged with adaptive optics and the cone classes identified through selective bleaching (Roorda & Williams, 1999). This has allowed direct measurements of the cone distributions and their variations across observers. The L:M ratio can also be inferred from the individual's photopic luminance sensitivity, since this depends on the summed responses of the L and M cones and thus varies with their ratio (de Vries, 1949; Lennie, Pokorny, & Smith, 1993). Another method which provides highly accurate estimates of the L:M ratio is the electroretinogram, which uses electrodes placed on the cornea to measure the electrical potentials generated by the retina in response to light (Brainard et al., 2000; Hofer et al., 2005).

Postreceptoral differences. We know much less precisely about the many possible ways that individuals routinely vary in the color pathways beyond the receptors, and how this might influence spectral sensitivity. Studies of the development and aging of the visual system reveal large life-span variations in sensitivity that occur at many levels of the visual pathway (Brown & Lindsey, 2004; Owsley, 2011; J.S. Werner, 1996). With aging these include large-scale cell loss and increased neural noise, so that the visual system is effectively operating as if at dimmer light levels (J. S. Werner et al., 1990). Changes have also been reported more centrally in factors such as weakened cortical inhibition, which reduces the stimulus selectivity of individual neurons (Schmolesky, Wang, Pu, & Leventhal, 2000). As noted, these age-related changes in color vision are considered in detail in chapter 32, but the variations revealed by such studies also point to likely ways that postreceptoral color mechanisms differ among individuals of similar age and thus which contribute to normal variations in color vision. For example, observers vary widely in the extent to which contrast adaptation reveals “higher-order” color mechanisms, and this may reflect large individual differences in the properties of cortical adaptation to color (Elliott, Werner, & Webster, 2012).

Personalizing color space

Most color metrics and color spaces are necessarily based on measurements averaged across many individuals to define a “standard observer.” From the foregoing, it is obvious that this standard does not necessarily describe the color vision of any real observer, and may poorly approximate the characteristics of many. For this reason, accurate assessments of color vision often require empirically measuring the spectral sensitivity of the observer. The extent to which this is warranted depends on how important it is to correctly calibrate the physiological effects of the stimulus for the task at hand. For example, in some tasks dominated by luminance cues (e.g. sensitivity to movement (Lindsey & Teller, 1990) or fine spatial patterns (Mullen, 1985)), even small errors in the relative luminance of two colors is sufficient to drive the performance, and thus could incorrectly characterize the performance based on the chromatic differences. Considerable effort has thus gone into developing methods to calibrate the stimulus for the observer.

As an illustration of these empirical approaches, consider the color space in Figure 3, which is derived from the MacLeod-Boynton chromaticity diagram (MacLeod & Boynton, 1979), and represents the stimulus in terms of an achromatic or “luminance isolating” axis (L+M+S) and two equiluminant chromatic axes corresponding to the opposing signals in the L and M cones (L-M) or the S cones opposed by both L and M (S-(L+M)) (Derrington, Krauskopf, & Lennie, 1984). These axes represent the principal dimensions and physiological pathways along which the cone signals are carried within postreceptoral neurons in the retina and geniculate, and many

studies have explored the visual information that can be carried by these dimensions (Livingstone & Hubel, 1988). However, testing this depends on choosing stimuli that isolate the responses of each pathway.

Figure 2

To isolate chromatic signals, the stimulus intensities need to be matched to maintain a constant luminance (Lennie et al., 1993). This adjustment for individual observers has been termed “sensation luminance” to differentiate it from the standard observer measure of luminance defined photometrically (Kaiser, 1988). Several ingenious techniques have been devised to measure the relative luminance of two colors and are widely used in studies of color vision. They generally depend on the differential sensitivity of the visual system to spatial and temporal variations defined by luminance or chromatic contrast. One classic method that was used to help define the CIE standard observer is “heterochromatic flicker photometry,” in which the two chromaticities are rapidly alternated in time (Wyszecki & Stiles, 1982). At appropriate rates, the perceived colors fuse but observers can still detect achromatic flicker, which can be nulled by matching the relative luminances. A second popular approach is the “minimum motion” technique, in which a luminance-varying and color-varying grating are alternated in spatiotemporal quadrature phase (Cavanagh, MacLeod, & Anstis, 1987). Luminance differences between the component colors in the color grating combine with the signals in the luminance grating to generate perceived motion in one direction or the other depending on the luminance differences between the two color components. Equiluminance is defined as the luminance ratio where the motion is nulled. Still another classic technique is the “minimally distinct border,” where the relative luminance of the colors making up two sides of an edge are adjusted until the edge appears blurriest (Boynton & Kaiser, 1968). An advantage of each of these techniques (over the more intuitive approach of simply equating the perceived brightness) is that the measured luminance function is linear. Thus the relative luminances of three non-collinear points are sufficient to define the entire equiluminant plane.

Isolation of the two chromatic axes for individual observers is attempted much less often, yet again these will often deviate from the axes predicted by the standard observer, in part because of lens and macular pigment screening. One method to identify the S-(L+M) axis has again been the minimally distinct border. This axis isolates signals in the S cones, and their sparse distribution results in the least visually distinct edges (Tansley & Boynton, 1976). A second method is based on selectively adapting the cones with different wavelengths (Webster, Miyahara, Malkoc, & Raker, 2000a). Short wavelengths differentially reduce sensitivity in the S cones and thus should produce the largest threshold changes in lights visible only to the S cones. Conversely, longer wavelengths adapt the L and M cones and thus result in thresholds that are maximally elevated along the L-M axis. Still another technique has been to employ transient tritanopia, a form of post-receptoral adaptation that leads to saturation in an opponent-channel response to signals from the S cones (Smithson, Sumner, & Mollon, 2003).

A final common step in empirically defining an individual color space is to adjust the relative strength of signals along the different axes so that observers are equally sensitive to a stimulus change along each axis. There is no a priori metric for this since sensitivity to the different axes varies widely and depends on the spatiotemporal structure of the stimulus. A typical solution is to scale each axis so that the signals are equivalent multiples of their respective detection thresholds for the observer (e.g. (Switkes, Bradley, & De Valois, 1988; Webster & Mollon,

1994)). For example, thresholds can be measured for detecting a change from gray in luminance or in chromaticity along either the L-M or S-(L+M) axes, and these thresholds can then be used to define a unit distance along each direction, so that the axes are equated for relative sensitivity. Another method involves direct contrast matching across different axes to equate the stimulus salience (Switkes, 2008). In this case, a fixed contrast of one pattern (e.g. a luminance grating) is matched by adjusting the contrast of a pattern varying along a different direction in color space (e.g. a grating defined by chromatic variations along the L-M axis) until the two patterns appear equally “strong.”

Individual differences in color appearance

Individual differences have been explored extensively with regard to color appearance. Here again there can be dramatic differences in how two individuals respond to the same stimuli.

Achromatic settings. The chromaticity that appears gray holds a special place in color vision because it is the neutral percept that all other colors are perceived relative to, and thus anchors all of color space. This anchor varies reliably across observers (R. D. Beer, Dinca, & MacLeod, 2006; Chauhan et al., 2014; Panorgias, Kulikowski, Parry, McKeefry, & Murray, 2012; Webster & Leonard, 2008; J. S. Werner & Scheffrin, 1993), and may even vary depending on the observer’s experience with different objects (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006) (see chapter 28). Differences in achromatic loci are largest along a bluish-yellowish axis, and smallest in terms of reddish-greenish differences. Notably, this pattern parallels variability within individuals, whose repeated white settings also tend to show more spread along a blue-yellow direction.

Unique hues. A large number of studies have measured the stimuli corresponding to unique hues – lights that appear pure blue, green, yellow, or red. A consistent finding is that individuals vary widely in the chromatic directions that are perceived as unique hues. For example, across a number of studies the inter-observer differences in the wavelengths selected vary from ~465 to 495 nm (blue), ~490 to 560 nm (green), and ~570 to 590 nm (yellow) (R. G. Kuehni, 2004). Large differences are also found when observers are tested with more broadband stimuli such as computer displays or printed palettes, which also reveal comparable variations in the locus of unique red (which is an extraspectral stimulus and thus does not correspond to a single wavelength) (Hinks, Cardenas, Kuehni, & Shamey, 2007; Miyahara, 2003; Webster, Miyahara, Malkoc, & Raker, 2000b; S. M. Wuerger, Atkinson, & Cropper, 2005). For example, another way of characterizing the spread of unique hues is in the range of angles they occupy within color space. When plotted in a threshold-scaled space such as Figure 2c (i.e. when sensitivity to color differences along the two axes of the space have been equated), the unique hues range from ~-10 to +10 deg for red, ~170 to 240 for green, ~-70 to -30 for yellow, and ~120 to 160 for blue (Webster et al., 2000b) (Figure 3). Variations in unique green are especially large, covering nearly 25% percent of the spectrum of visible wavelengths. Some early reports suggested that these might exhibit a bimodal distribution pointing to two classes of individuals (Richards, 1967). Other studies have failed to replicate this pattern (Jordan & Mollon, 1995; Volbrecht, Nerger, & Harlow, 1997; Welbourne, Thompson, Wade, & Morland, 2013), though one recent report found possible evidence for multiple clusters (Abramov, Gordon, Feldman, & Chavarga, 2012).

Figure 3

Differences in unique hues are also found at the population level. For example, a comparison of observers in India and the US showed systematic differences in the stimuli chosen for unique or focal colors (Webster et al., 2002). These differences also occur within the World Color Survey, a monumental survey of color naming in 110 disparate languages throughout the world (Kay, Berlin, Maffi, Merrifield, & Cook, 2009) (see chapter 7). The foci of corresponding color terms across different linguistic groups (e.g. terms paralleling English “red” or “blue”) can again point to subtly but significantly different stimuli (Webster & Kay, 2007).

Binary hues. Individual differences in color appearance also extend to binary hues – hues such as orange or purple that appear as mixtures of the unique hues (e.g. red and yellow, or red and blue). Variability in these judgments is comparable to the variations in the unique hues (J. M. Bosten & Lawrence-Owen, 2014; Malkoc, Kay, & Webster, 2005) (Figure 3). This is unexpected if the binary hues are implicitly represented by the independent responses in mechanisms that explicitly signal pure red-green or blue-yellow sensations. Further, the range of settings is so wide that the distributions of unique and binary hues overlap (Malkoc et al., 2005). This means that what one observer chooses as a balanced orange, another might choose as a pure red or yellow (see Figure 4). Still more surprising is that the loci of the binary mixtures are uncorrelated with the unique hues, which in turn are uncorrelated with each other. Thus knowing someone’s choice for unique yellow does not predict what they will select for unique red, and even knowing both their yellow and red does not predict their orange (Abramov et al., 2012; Hinks et al., 2007; Malkoc et al., 2005; Miyahara, Szewczyk, & McMartin, 2004; Webster et al., 2000b).

Color naming. Individual differences have further been evaluated for the full palette of hues by comparing how people differ in how colors are labeled. Lindsey and Brown analyzed color naming of participants in the World Color Survey, but focused on the patterns across individual respondents rather than the aggregate responses of different linguistic groups (Lindsey & Brown, 2009). There are enormous variations within groups (Webster & Kay, 2007), and intriguingly, these could be characterized by a small number of individual “motifs” or patterns of partitioning color space. These motifs complement cross-cultural similarities in color naming by revealing cross-individual strategies for labeling colors that transcend language. That is, individuals speaking the same language might categorize the palette of colors in very different ways, while speakers of different languages might label them in similar ways.

Gender differences. A large number of studies have examined differences in color appearance between males and females (e.g. (Abramov et al., 2012)). A recent motivation for this work is the realization that the genetics of the cone pigments is more variable in females who might be heterozygous for normal or anomalous variants of the L and M genes, as noted above. Such females have been reported to make finer categorical distinctions across the spectrum, dividing it into more than the seven traditional bands of the rainbow described by Newton (Jameson et al., 2001) (though this color naming difference on its own does not require tetrachromacy). However, a recent analysis of female carriers of deuteranomaly, who should express four distinct pigments, found only one of 24 tested showed evidence for greater dimensionality in both her color discrimination and color experience as assessed by multidimensional scaling (Jordan et al., 2010). Further studies based on multidimensional scaling have revealed gender differences in color experience in which a red-green dimension has greater salience for females while lightness variations are more salient for males (D. L. Bimler, Kirkland, & Jameson, 2004), with female carriers for color deficiency also showing reduced red-green salience (D. Bimler & Kirkland,

2009). Several studies have also found gender differences in hue judgments such as the unique hues (Abramov et al., 2012; R.G. Kuehni, 2001; Volbrecht et al., 1997). Moreover, these differences have further been observed in how color percepts change in peripheral viewing (Murray, Parry, McKeefry, & Panorgias, 2012).

The relationship between sensitivity and appearance

The presence of pronounced normal variation in both sensitivity and appearance begs the question of how the two are related, and as we have noted, many studies have approached measurements of appearance motivated by prospects of finding perceptual correlates of genetic or physiological differences in color coding. However, the link between appearance and sensitivity remains tantalizingly obscure, in part because the neural basis of color percepts has itself remained elusive. For example, it is currently controversial whether the visual system encodes color within mechanisms that directly mediate the perceptually unique hues (J. D. Mollon, 2009; Stoughton & Conway, 2008), and among theories that assume this, the perceptual mechanisms have been placed both very early and very late in the visual pathway (De Valois & De Valois, 1993; Schmidt, Neitz, & Neitz, 2014). Thus there is currently little consensus about how the structure of color experience is instantiated in the brain. Yet individual differences have nevertheless pointed to some of the principles that are likely to be fundamental to this structure.

Achromatic settings. As described above, individual differences in spectral sensitivity are pronounced, not only between observers but also within observers in different parts of the visual field. Strikingly, however, these differences completely fail to predict the stimulus that observers perceive as white. The clearest examples of this disconnect are with the inert screening pigments. As we noted, the lens pigment density increases steadily with age, so that the spectrum reaching the receptors is increasingly filtered at shorter wavelengths. If young and old observers based their perception of white on the same retinal stimulus, then the world should appear increasingly yellower with time (J. S. Werner et al., 1990). Yet as a group older observers instead continue to perceive the same physical stimulus as white that their younger counterparts choose (J. S. Werner & Scheffrin, 1993). Similarly, the light spectrum reaching the receptors in the fovea and surrounding periphery is different because of the spatial distribution of macular pigment. Yet the perception of white again remains constant for a constant physical stimulus across much of the visual field (D. Beer, Wortman, Horwitz, & MacLeod, 2005; Webster & Leonard, 2008).

Unique hues. Similar dissociations between sensitivity and appearance are found for hue percepts. For example, the loci of unique hues also remain constant with age despite the large senescent changes in vision (Scheffrin & Werner, 1990; S. Wuerger, Xiao, Fu, & Karatzas, 2010), and also remain much more stable in the periphery than predicted by differences in macular pigment screening (Webster, Halen, Meyers, Winkler, & Werner, 2010). These effects run counter to suggestions that differences in color percepts might be closely tied to variations in short-wave sensitivity. For example, Lindsey and Brown noted that languages that lack separate terms for blue and green tend to occur in regions of the world with high UV exposure, and proposed that the reduced color terms might reflect greater brunescence of the lens and S cone damage (Lindsey & Brown, 2002). However, older observers with these losses fail to show the predicted reductions in color naming (Hardy, Frederick, Kay, & Werner, 2005).

A number of studies have explored the relationship between unique hues and cone ratios. The L:M ratio could in theory set the null point of a “red-green” perceptual channel (Cicerone, 1987).

However, variations in this ratio do not predict individuals' unique yellow settings (Brainard et al., 2000; Miyahara, Pokorny, Smith, Baron, & Baron, 1998; Pokorny & Smith, 1987). Hue percepts also cannot be predicted from variations in the spectral peaks of the cones, for example in anomalous trichromats (Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002; Pokorny & Smith, 1977). Moreover, most retinal sources of sensitivity variation impact wavelengths throughout the spectrum and thus should have broad impact on color appearance (Webster et al., 2000b). Yet as noted, the variations in unique hues are instead independent, suggesting that there is little influence of a common factor. However, the potential links between unique hues and sensitivity may be complex and thus difficult to unravel. As an example of this complexity, Jordan and Mollon proposed that individual differences in unique hues were in fact tied to differences in spectral sensitivity, but only when observers are tested with narrowband spectra (Jordan & Mollon, 1995; J. D. J. Mollon, G., 1997). By this account, observers learn to associate concordant color names with natural broadband spectra, even though their eyes filter these spectra in different ways. With these spectra, individual differences are thus expected only insofar as there are differences in the learning. However, when the same observers are now shown monochromatic lights – which their pigments no longer differentially filter - each must choose a different wavelength to match the relative cone responses to the broadband stimulus. This predicts that unique hues should be correlated with factors like the density of pigments in the retina, and weak correlations of this kind have been reported for unique green (Jordan & Mollon, 1995; Welbourne et al., 2013). However, other studies have found little change in the unique hues as spectral bandwidth varies (Mizokami, Werner, Crognale, & Webster, 2006), and moreover, that variability in the unique hues remains pronounced for the less saturate spectra that individuals normally experience (R.G. Kuehni, 2001; Webster et al., 2000b).

Adaptation and individual differences

The foregoing shows that two observers with very different spectral sensitivities can nevertheless describe the appearance of spectra in similar ways. Such results point to mechanisms which somehow discount the idiosyncrasies of the individual's eyes from their reported experience of color. What are these mechanisms? One possibility, as suggested above, is that they reflect learning, and that individuals have been taught to label similar stimuli in similar ways, even if these labels correspond to different sensations. For example, the stimuli that appear as unique hues could reflect special characteristics of the environment rather than special states in the neural responses to color. Consistent with this, the average loci of unique blue and yellow lie suspiciously close to the daylight locus (J. D. Mollon, 2006), and the foci of basic color terms fall close to how color signals might cluster in natural images (Yendrikhovskij, 2001). Learning effects are likely to be especially important for understanding differences in color naming, since the categories an individual learns may depend on the stimulus distinctions that are important to their culture or trade (Komarova & Jameson, 2008; Lindsey & Brown, 2009).

However, another form of learning is that the visual system adjusts to compensate for variations in sensitivity, through processes of adaptation. Adaptation is in fact ubiquitous in sensory coding, and effectively calibrates neural responses so that they are matched to the ambient stimulation (Webster, 2011). In color vision this sensitivity regulation is known to occur at multiple sites and adjust to multiple properties of the stimulus, including retinal adaptation to the average chromaticity and cortical adaptation to the gamut or variance of color signals in the stimulus (Webster, 1996). Retinal adaptation begins as early as the photoreceptors, which each

independently light adapt or adjust their gain according to the average light exposure (a process known as von Kries adaptation). A process like von Kries adaptation can factor out the average color of the stimulus, and thus can contribute to approximate color constancy when the illumination changes (Brainard & Wandell, 1992). That is, if the light gets redder, then the sensitivity to red decreases, so that over time the world will again appear gray. The same adjustments can also occur when the observer changes, again promoting perceptual constancy. As the density of lens pigment increases, S cones will on average receive less light, and thus their sensitivity will increase (J.S. Werner, 1996).

Adaptation adjustments of this kind may play a central role in compensation for sensitivity differences between observers or within the same observer at different retinal locations. For example, Webster and Leonard compared achromatic settings and adaptation in the fovea and near periphery (Webster & Leonard, 2008). The white settings remained very similar despite the differences in macular pigment screening. But more importantly, the stimulus that was neutral for adaptation (i.e. did not induce a color aftereffect) was also equivalent at the two loci. This reveals that the neural compensation for spectral sensitivity differences had already occurred at or before the site of short-term chromatic adaptation. Since as we noted the chromatic adaptation is primarily at the level of the receptors, this suggests that the cones themselves are adapted to the average spectrum that they are locally exposed to. Similar adjustments over time can in principle account for much of the stability in color appearance as the lens density changes with aging. However, it may not account for all of the change. Color constancy between the fovea and periphery, or between young and old observers, is not perfect, but is substantially better than predicted by adjustments to the average color alone (Bompas, Powell, & Sumner, 2013; Mizokami et al., 2006; O'Neil & Webster, 2014; Webster, Halen, et al., 2010; S.M. Wuerger, 2013). This suggests that additional compensatory processes correct color appearance for the sensitivity limits of the observer. Even adjustments for the average color may not reflect the same mechanisms underlying simple color aftereffects, for in some cases these adjustments follow a very slow time course. For example, Delahunt et al. tracked achromatic settings in patients after cataract surgery (Delahunt, Webster, Ma, & Werner, 2004). These took weeks or even months to return to values approaching the settings before surgery.

Again, the consequence of such adaptation processes is to factor out or discount the sensitivity limits of the observer. Thus these processes are important for trying to predict how color percepts might differ between observers. Many attempts have been made to simulate the perceptual worlds of individuals with variant color vision, for example with color deficiencies or sensitivity differences due to aging or development. However, typically these simulations merely filter out the color signals according to the reduced sensitivity of the observer, and fail to model the adjustments expected if observers are adapted for their sensitivity. When this adaptation is included the predicted perceptual differences between observers are much smaller (Webster, Juricevic, & McDermott, 2010). For example, the right hand images in Figure 1 show the predicted effects of changing the lens or macular pigment densities after assuming von Kries adaptation to the spectral changes. This simple step alone removes most of the pigment screening effects from the observer's color experience.

However, we are left with the problem that observers do not report seeing color in similar ways – that there are pronounced differences in almost all measures of color appearance. As noted, the basis for these differences remains uncertain, yet adaptation may again play a role, for

differences are expected if observers are adapted to different color worlds. Natural environments do vary widely in both their mean chromaticity and color gamut, and moreover the same environment varies over time as the weather or time of day or seasons change (Granzier & Valsecchi, 2014; Webster, Mizokami, & Webster, 2007; Webster & Mollon, 1997). Thus observers exposed to different environments should be adapted in different ways. These can again include both short and longer-term changes in color perception (Belmore & Shevell, 2008; Juricevic & Webster, 2009; Neitz et al., 2002; Webster & Mollon, 1997). For example, Figure 4 simulates how a lush or arid environment might appear to an individual living in and thus adapted to each environment. The simulation was based on a model of color adaptation in the human visual system and how it would adjust to the distribution of colors characteristic of different color environments (Juricevic & Webster, 2009). Note that the predicted effect is to reduce the salience of dominant colors in each setting while enhancing the salience of more novel colors.

Figure 4

Such adaptation effects have philosophical implications for individual differences and the problem of other minds - whether two individuals might have the same perceptual experiences and how we could know. First, the adaptation is asymmetric, insofar as it is the observer that is adapted to the stimulus (Webster, Werner, & Field, 2005). Thus to the extent that observers are exposed to a common color environment, their adaptation states and some aspects of their perceptual experience (e.g. the stimulus that appears neutral or a norm) should converge, even if the physiological characteristics of their visual systems are very different. Conversely, if they are adapted to different environments, then at least some aspects of their color perception (e.g. again the stimulus that appears a neutral gray) should diverge, even if they are physiologically very similar. The second implication is that these differences in part depend on – and thus are potentially predictable from – the properties of the world, independent of the observer. Thus whether two observers have shared or unique color experiences – particularly with regard to their perceptual norms - can in principle be partly determined by objective measures of the physical world outside them rather than the private mental world within (Webster et al., 2005; Webster, Yasuda, Haber, Ballardini, & Leonard, 2007).

Acknowledgments

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Figure Legends

Figure 1. top: Simulations of normal variations in lens pigment density. a) image as seen by a younger reference eye; b) the same image filtered through the eye of an observer with the average lens density of a 70 year old; c) the image as seen by the older observer adapted to their lens pigment density. bottom: simulations of normal variations in macular pigment density. a) an image seen foveally; b) the same image as seen in the periphery with the screening by macular pigment removed; c) the peripheral image assuming the receptors in the periphery are adapted to the average spectral stimulus at their location. Adapted from Webster, M. A., I. Juricevic and K. C. McDermott (2010). "Simulations of adaptation and color appearance in observers with varying spectral sensitivity." *Ophthalmic Physiol Opt* **30**(5): 602-610.

Figure 2. Calibrating color space for the individual spectral sensitivity of the observer. a) The standard 3 dimensional color space. The tilt defining the plane of constant luminance varies across observers and thus is usually estimated empirically; b) equiluminant plane defined by the nominal L-M and S-(L+M) cardinal axes. The ellipses show contrast thresholds measured on different chromatic backgrounds to try to isolate the actual cardinal axes for the individual; c) The equiluminant plane scaled to equate perceived contrast along different axes. With the wrong scaling (ellipse) contrast systematically varies with angle in the plane. Adapted from Webster, M. A., E. Miyahara, G. Malkoc and V. E. Raker (2000). "Variations in normal color vision. I. Cone-opponent axes." J Opt Soc Am A Opt Image Sci Vis **17**(9): 1535-1544.

Figure 3. Unique hues and binary hues selected by a group of color-normal observers, plotted as angles in the cardinal axis space. a) all observers; b) observers who showed the highest reliability in repeated settings. From Malkoc, G., P. Kay and M. A. Webster (2005). "Variations in normal color vision. IV. Binary hues and hue scaling." J Opt Soc Am A Opt Image Sci Vis **22**(10): 2154-2168.

Figure 4. Simulations of the color appearance of lush or arid environment to observers adapted to each environment. Top: original images; Bottom: the same images after modeling adaptation to the distribution of colors characteristic of each environment. From Webster, M. A. (2011). "Adaptation and visual coding." J Vis **11**(5): 3: 1-23.

Figure 1

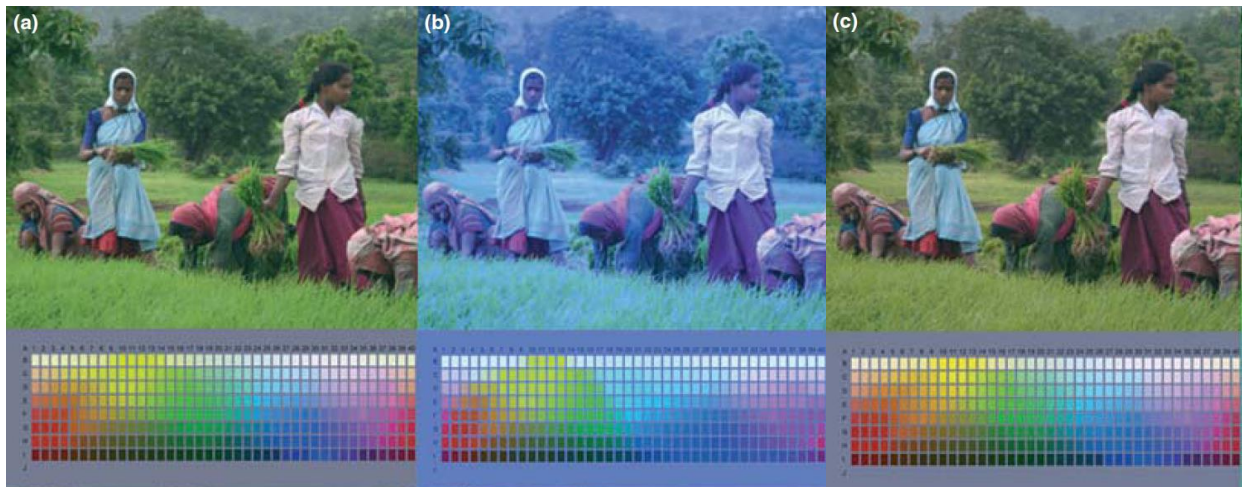


Figure 2

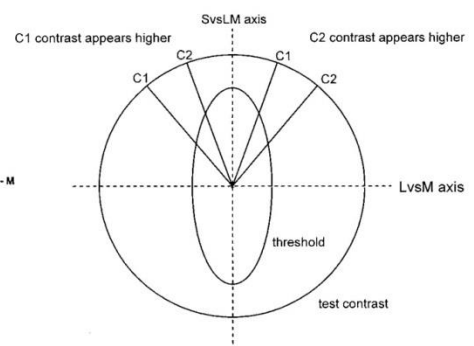
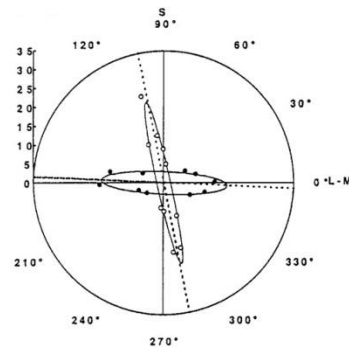
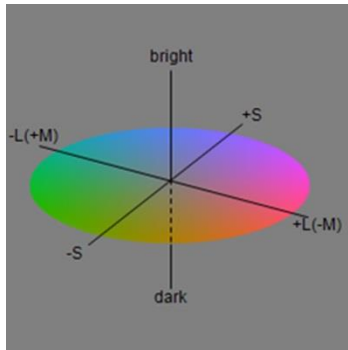


Figure 3

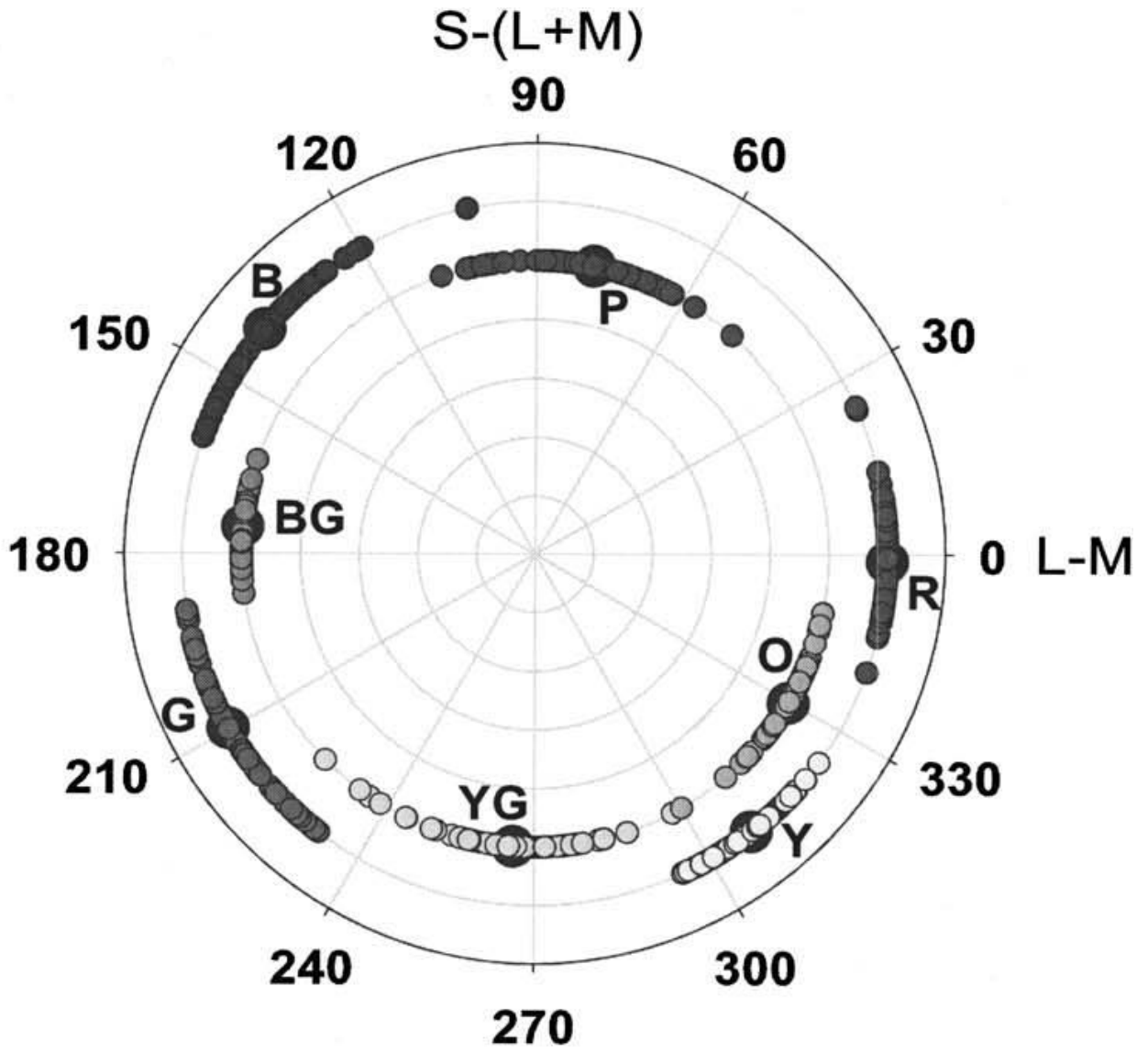


Figure 4

